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THE FORMATION OF THE COMMERCIAL STOCK OF THE NORTH ATLANTIC ROCK GRENADIER

By V.V. Dushchenko of the Polar Scientific Research Institute of Marine Fisheries and Oceanography (PINRO)

Despite the many studies that have been devoted to the rock grenadier of /141* the North Atlantic, many aspects of its biology remain unknown; in particular, various opinions exist as to the population structure of this species, its migrations and the source of recruitment of the commercial stock of the Northwestern Atlantic (NWA), where almost exclusively sexually-immature fish are caught. The hypothesis of the transport of the grenadier roe and larvae to the Canadian continental slope from the Iceland region has become the most popular (Zakharov, Mokanu, 1970), although the possibility of a reverse migration remains controversial. In this connection, we have made an attempt to determine the degree of isolation of rock grenadier groupings by the methods of biochemical genetics and enlisting other materials as well.

The structure of populations was investigated by polymorphous loci of nonspecific esterases of muscle tissue (Nefedov et al., 1976), sorbitol dehydrogenase (SDH) and NADP-dependent malate dehydrogenase (ME). We used the method of /142 electrophoresis in polyacrylamide gel. Dilution was done in a uniform buffer

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system (Peacok et al., 1965). Ten percent gel and 6% SDH and ME were used to obtain the spectrum of the esterases. The phoregrams were stained by the usual methods.

The electrophoretic spectra of SDH and ME are shown in Fig. 1, A,B. It is assumed that the synthesis of each of these proteins is controlled by a tetra -allelic locus. In both cases, the frequency of the most and least mobile allelic forms is small. The electrophoretic spectra of the esterases have been obtained in only 30 samplings of 4,234 muscle tissue specimens, SDH in 19 samplings of 2,846 specimens and ME in 10 samplings of 1259 specimens.

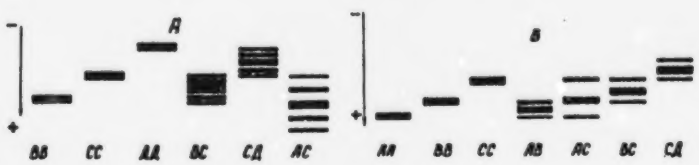

Fig. 1. Electrophoretic variants of SDH (A) and ME (B) of rock grenadier muscle tissue.

Good agreement was usually noted between the obtained and theoretical distribution of SDH and ME phenotypes. A disequilbrium of samplings in terms of the concentrations of the phenotypes of the esterases was found rather often. Comparison of the local frequencies of the genes and the genotypes of the three loci studied in some cases made it possible to ascertain differences between particular samples, but these subsequently proved to be unstable. For example, reliable changes in the concentrations of the esterase phenotypes ($x^2 = 12,775$; $p = 0,99$) were noted in two samples of grenadier from the Bill Bailey'6* Banks (Faeroes Is. region). A similar phenomen was observed at one of the banks of the Reykjanes* ridge. In this case, the differences did not reach the level

*Spelling approximate. - Transl.

of significance, but the initial isolation of one of the samples was not borne out.

Analysis of the causes of the variation in the allelic and phenotypic frequencies in some regions revealed that this is due to their fluctuations in particular size groups. Moreover, reliable differences in the concentrations of esterase alleles are observed even between adjacent 5-cm classes. This type of variability has been observed in both males and females, and when the difference /14
in the rate of growth is taken into consideration, the fluctuations in the allelic frequencies are synchronous in fishes of the same generation.

On repeated genetic analysis of the grenadier from a particular region, a similarity in the curves of distribution of the allelic frequencies of the esterases in difference size groups is usually observed. For example, in 1979, two grenadier samples each were obtained from the regions of Baffin I. and Northern Labrador. Despite their small volume (100 specimens each), maxima and minima of gene concentrations that are characteristic of a definite habitat were found in each of them. This made it possible to combine them in pairs and to examine them as a whole (Fig. 2, curves 7 and 8).

The two samples collected from the George Bligh* banks (Faeroes Is. region) are also similar: in both cases, an excess of the homozygote E_{st}-I_c in fish measuring 71-75 cm is quite distinct. A sample of grenadier of the Hutton* /144
plateau, obtained at the same time 30 miles to the west, showed no such disorders. It is evident that the detected fluctuations in the allelic frequencies of the esterases depending on fish size allow us to distinguish inidivudal grenadier groupings and are also indicative of their localization and heterogeneity. However, the broad application of this method of distinguishing isolated grenadier stocks

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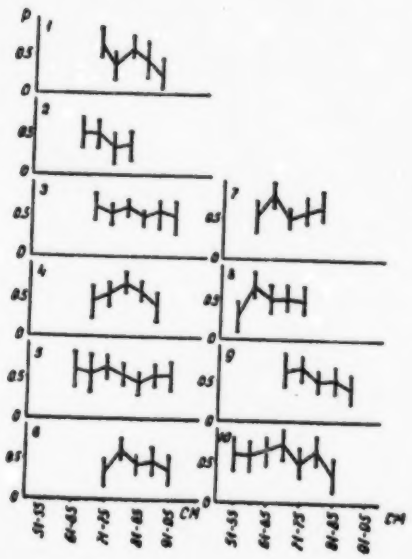

Fig. 2. Variability in concentrations of the E_{st}-I_c gene in rock grenadier males in particular samples depending on size:

1 -6 - some banks of Middle Atlantic Ridge (MAR); 8 - Baffin I.; 8 - Northern Labrador; 9 - Bill Bailey's banks; 10 - Rockall*plateau.

involves some limitations, and in particular, it is necessary that all sub-units /144 that make up a given grouping be represented equally in the analyzed samples. It is difficult to guarantee that this condition is met, especiallyon the banks of the MAR (Middle Atlantic Ridge), where the catching of only some part of an accumulation is possible because of peculiarities in fish distribution. It is

because of this, for example, that two samples, obtained from the same point on the ridge at an interval of less than 1 month, shown on Fig. 2 in curves 3 and 3, do not show a similarity. Their qualitative difference is also obvious upon analysis of the sex ratio : in one, there is almost 100% males, in the other, less than half.

At the same time, despite the high variability in the concentrations of the alleles of the esterases depending on fish size and the isolation of some samples, on the whole for the range, the concentrations of genes and genotypes of the three polymorphous loci remain almost unchanged. This is obvious when the total samples for the three main fisheries regions are compared (Table 1).

Although the grenadier grouping of the Northeast Atlantic(NEA) differs from those living on the ridge and the Canadian continental slope, respectively, in the distribution of the phenotypes of esterases ($x^2 = 16.460$; $p = 0.99$) and the concentrations of the gene ME_c ($t = 2.137$), the actual discrepancies are small and on the whole reflect neither the isolation of these regions by deep-water zones, nor the differences in their ecological conditions. The latter is especially evident when materials on the grenadier of the northern parts of the MAR and NWA are compared. They can be assigned to a single aggregate in terms of the distribution of allelic and phenotypic frequencies, although the differences in the geological features of the habitats are obvious; hydrological conditions also do not correspond. In addition, the grouping of the Canadian continental slope consists almost exclusively of sexualy immature fish. Similar results have evidently been obtained on analysis of the gene frequencies of polymorphous loci of the myogens, phosphoglucomutase and α-glycerophosphate dehydrogenase.

Despite the genetic heterogeneity of the samples found, regions of /146 gene concentrations characteristic of grenadier groupings of a particular area have not been distinguished (Lovinenko et al., 1981).

TABLE 1

Phenotypic and allelic frequencies of esterases, SDH and ME in rock grenadier samples from the main fisheries regions of the North Atlantic.

region		Phenotypes BB	BC	CC	rare	n	x^2	Alleles A	B	C	X
						esterases					
NWA	n	249	297	224	25	795	42,343	0,0I6	0,509	0,474	0,00I
	p	0,3I3	0,374	0,282	0,03I						
MAR	n	5I5	552	477	50	I594	I30,239	0,0I4	0,50I	0,48I	0,004
	p	0,323	0,346	0,299	0,032						
NEA	n	564	744	465	72	I845	45,424	0,0I7	0,5I6	0,462	0,005
	p	0,306	0,403	0,252	0,039						
						SDH					
NWA	n	23	I45	592	27	787	I4,I24	0,006	0,I2I	0,860	0,0I3
	p	0,029	0,I84	0,752	0,035						
MAR	n	28	I56	670	22	876	23,069	0,00I	0,I22	0,864	0,0I3
	p	0,032	0,I78	0,765	0,025						
NEA	n	24	I97	927	35	II83	I3,II8	0,002	0,I04	0,880	0,0I4
	p	0,020	0,I66	0,784	0,030						
						ME					
NWA	n	98	I35	95	I7	345	I0,276	0,020	0,495	0,48I	0,004
	p	0,284	0,39I	0,275	0,050						
MAR	n	I33	I74	II0	28	445	II,I23	0,027	0,509	0,458	0,006
	p	0,299	0,39I	0,247	0,063						
NEA	n	I40	I96	94	39	469	2,608	0,035	0,530	0,428	0,007
	p	0,296	0,4I8	0,200	0,084						

This indicates that despite the definite localization of grenadier /146
accumulations, a constant and intensive exchange of genetic material is going on among them. The method by which it takes place is also hypothesized. The transport of pelagic roe and larvae of this species by oceanic currents, although not having been widely discussed in the literature, seems not to meet with any particular objections. The possibility of this phenomenon in grenadiers has been confirmed by the works of a number of authors (Marshall, 1965; Merrett, 1978). At the same time, the results of the genetic-population analysis and a number of other data cast doubt on the reality of regular extensive migrations of grenadier more than 15-20 cm long.

Thus, the morphometric investigations have revealed differences in the fishes caught in different complexes of banks of the MAR in the adjusted brain mass, barbel length and number of rays in the dorsal and pectoral fins. Three local groupings have been distinguished as a result (Galaktinova, 1978). The grenadier of the northern and southern part of the ridge also differs in the relative mass of the otoliths: they are lighter in fishes dwelling in the north. In addition, a local reduction in catches per hour of trawling and a reduction in the average grenadier length has been observed for a number of years on the Northern Newfoundland banks as a result of the excessive fishery on a limited area (Savvatimskii, 1972).

Especially indicative are differences in the sexual composition of the catches of this species in particular regions. Thus, from the Bill Bailey's banks to the southwestern part of the Rockall plateau. the number of males in catches increases regularly on average from 46 to 67%. These differences were observed rather regularly from 1976 to 1980. They cannot be explained by a subdivision of the range into trophic, reproductive and other parts and are clearly

not due to insurmountable obstacles for the grenadier. For example, the distance between the 500-m isobaths on the Bill Bailey's banks and the Outer Bailey banks is only about 20 miles, while the depths separating them do not much exceed 1000 m, and form part of the zone inhabited by this species, but in the former, the males made up less than half of catches over 5 years, while they predominated in the latter.

Certain aspects of the biology of the grenadier also give no basis to assume the possibility of extensive migrations of the adult fish. /147 But despite the insufficient study of the conditions of the formation of its accumulations, we may assume that they correspond to the general patterns of fish distribution in the open part of the sea (Darnitskii, Boldyrev, 1977; Amarov, Elizarov, 1982), which are determined by the dynamics of waters and the conditions of accumulation of forage objects. A coincidence in concentrations of deep-water plankton and grenadier has been noted in the region of a cyclonic gyral (Strogonov, Samchik, 1979). It has also been established that the grenadier avoids passive transport by currents and can linger in a favorable zone, making vertical migrations and using the slopes of underwater elevations as a screen (Kemenev, 1979; Vinichenko, 1979).

Considering the great influence of floor relief on the dynamics of waters and the formation of concentrations of forage organisms (Kotenev, Matishev, 1972; Popova, 1977), as well as the attachment of the grenadier to the bottom, we might expect the same constancy in the localization of stocks as, for example, in the cod of the Grand Newfoundland banks (Bulatova, Turuk, 1979). The lack of essential differences in the size-age make-up and physiological condition of the fishes in different accumulations on most of the range also does not contradict this. The only exception is the sexually-immature grenadier of the

northern part of the Canadian continental slope. It is the existence of this grouping, and the necessity of determining its status, that gave rise to the migration hypothesis, which we should discussin more detail.

Its adherents (Zubchenko, 1981) suppose that some of the larvae are carried by the current from the spawning grounds on the ridge into the Devisov strait and are distributed along the coast of Canada. As the grenadier grows, it shifts from Baffin I. and Labrador to the region of the Northern Newfoundland banks and the Flemish Cape banks, from which it makes a spawning migration to the MAR and the Hutton plateau. The existence of a single population of this species with a subdivided range is thus hypothesized.

The examples of differences in grenadier groupings, including genetic differences, cited above, are not in accord with this hypothesis. In addition, although a relatively small number of sexually mature fishes (about 5%) have been found on the Flemish Cape banks, they had gonads in both the pre-spawning /148 as well as post-spawning state. Their distribution by stages of maturity essentially did not differ from that obtained on the MAR in a comparable period (Table 2). This indicates the existence of local small spawning grounds. In addition, long-term analysis of the size make-up of the NWA grenadier shows that its average length decreases from 63.8 cm in the region of Baffin I. to 56.1 cm in the region of the Northern Newfoundland banks (Savvatimsky, 1977). Nor has an increase in the number of large fish been noted on the Flemish Cape banks: the average length of males was 59.7 cm, females 62.8 cm in March, 1978.

The example of the local overfishing of the Northern Newfounland banks, through which the large fishes must pass from Labrador and Baffin I., which we discussed above, is also not in accord with the migration hypothesis. The improbability of a spawning migration of the NWA grenadier becomes even more obvious when one considers that the facts cited by its adherents can be interpreted

from opposite points of view. Thus, the changes in the infection of the grenadier by parasites (Zubchenko, 1981), may perhaps be due to seasonal variation and the subdivision of local groupings into smaller subunits.

TABLE 2

Distribution by stages of maturity of the sexually mature rock grenadier on the Flemish Cape bnaks and the banks of the northern part of the Middle-Atlantic Ridge in February-March, 1978, n/%.

stages of maturity	Flemish Cape banks		Middle Atlantic Ridge	
	males	females	males	females
II	49 / 47,6	21 / 20,4	35 / 22,3	40 / 25,5
IV	2 / I,9	-	35 / 22,3	-
V	4 / 3,9	-	I9 / I2,I	-
VI	4 / 3,9	-	I / 0,6	-
VI-II	4 / 3,9	I9 / I8,4	2 / I,3	25 / I5,9
Total	63 / 6I,2	40 / 38,8	92 / 58,6	65 / 4I,4

The widespread opinion as to a definite localization of commercial groupings of the rock grenadier (Marshall, 1965; Savvatimskii, 1972; Galaktionova, 1978; Dushenko, 1980) thus appears to be more justified. The quite understandable complexity of studying the ecology of deep-water fishes and the equalization of gene frequencies over the range because of the reduction in the extent of isolation /149

at the early stages of development, complicate the determination of their boundaries. However, the experience of the fishery on the Northern Newfoundland banks, as well as other factors oblige us to take a cautious attitude to the possibility of recruitment of some accumulations of this species due to migration of adult fish from other parts of the range. In this connection, it is now advisable to regard the grenadier groupings as localized, but to some extent or other replenished by the transport of roe and larvae by ocean currents. It appears that this approach not only accords better with the known facts, but will also help to more efficiently exploit the commercial stocks of this species at this stage of study.

Passing to the question of intraspecies structure, we must emphasize that the lack of reproductive isolation does not prevent us from distinguishing population units in the rock grenadier and does not cast doubt on their biological meaningfulness. The conception of the population as a group of individuals connected only with some one place of habitation (the biotope), constricts our understanding of the structure and function of this biological system. It is only certain age groups, year-classes or stages in development that very often turn out to be local (Shkorbatov, 1981). The study of the spatial structure of pelagic biocoenoses and the distribution of the species inhabiting them has demonstrated the possibility of applying the population approach in similar situations and has made it possible to develop a functional classification of the observed intraspecies structures (Belklemishev, 1969). That it is correct to distinguish populations in the rock grenadier is also confirmed by the fact that its groupings can react not only to the fishery, but also to specific environmental conditions, just as do populations in the classical sense: by variability of morpho-physiological characters and sex ratio, as well as by the appearance of genetic differences. In the latter case, several levels of differentiation can be noted.

As we have already noted, when the total allelic and phenotypic /150 frequencies of the esterases, SDH and ME are compared for the three main regions inhabited by the grenadier (see Table 1), they show a great similarity, but at the same time, the samples are sharply unbalanced because of the mixing of the representatives of the different inheritance groups (Vallund* effect). Unlike the total ones, the local concentrations of alleles of the study loci are more variable; the differences may sometimes be reliable, while the samples in most cases are well balanced. This has also been noted by other investigators (Logvinenko et al., 1981). However, the sharp fluctuations in the concentrations of the alleles of the esterases in some size groups and the observed reliable differences in this character even between adjacent 5-cm classes of the same sample indicate a genetic heterogeneity of local groupings as well.

The results obtained are in good agreement with the familiar approach to the biological species as a hierarchical system of coordinate populations, where genetic stability increases in proportion to complication of their structure (Altukhov, Rychkov, 1970). In this view, and taking into consideration data on the sex ratio in grenadier catches in addition to genetic morpho-physiological variation, we may propose a preliminary working scheme of the population structure of this species.

First of all, it is necessary to distinguish the geographic populations of the MAR, NWA and NEA. Their ranges are well demarcated by deep-water regions and have uniquely characteristic ecological conditions. Each geographic population comprises a number of local ones. The boundaries between them are probably conditional and are determined not so much by natural obstacles so much as by the ecological heterogeneity of the region, particularly, the circulation of water masses. The available data suggest that the mixing of adult fish belonging

*Transliterated. - Transl.

to different local populations is limited, and they are therefore regarded in the proposed scheme as basic units of the commercial stock. They are distinguished in each particular case on the basis of morphological variation, sex structure of catches, population dynamics and features of age-size composition. Genetic differences may also be manifested at this same level.

The variation in allelic frequencies depending on fish size indicates that the local populations are also heterogeneous and consist of a number of /151 groupings of the type of elementary or subpopulations (Lebedev, 1967; Altukhov, Rychkov, 1970). These are probably to a large extent temporary formations, although one cannot exclude their partially hereditary nature.

We may thus assume that the rock grenadier forms within its range a complex of populations, whose spatial structure is determined in many ways by the circulation of the waters of the North Atlantic. In functional structure, this complex is similar to those observed in two other species of Myctophidae (O'Day, Nafpaktitis, 1967), as well as in many pelagic organisms and benthic invertebrates with pelagic larval stage (Beklemishev, 1969). It would appear that the classification of populations based on their capacity for self-reproduction (independent, dependent and pseudopopulations), developed by K.V. Beklemishev is also quite applicable to rock grenadier groupings, and the conditions which he determined as causing a reduction in reproductive potential also correspond to those observed.

The establishment of an obligatory connection between the appearance of sterile pseudopopulations and the process of transformation of waters suggests that the transport of the grenadier from the temperate climatic zone of the Atlantic into waters formed under the influence of the cold Labrador current results in the fact that the individuals of this species cannot traverse the complete life cycle. The inadaptability of the grenadier to the conditions existing in the NWA is also confirmed by the fact that the fishes living there

have a slow rate of growth by comparison with others, as well as a mass which is smaller by almost half with identical length (Savvatimskii, 1969; Maucorps, Fontaine, 1979).

Considering the lack of convincing proof of the existence of a spawning migration of the grenadier of the northern part of theCanadian continental slope to the spawning grounds of the ridge, we may suppose that this geographic population is a dead-end which is completely dependent on recruitment from outside. In K.V. Beklemishev's functional classification, it can be regarded as a pseudopopulation.

The appearanceof a relatively small number of sexually mature fish on the Flemish Cape banks is also in agreement with this scheme. One of the branches of the Labrador current meets with the warm North Atlantic current in this region (Buzdalin, Elizarov, 1962). The mixing of these watersevidently creates more favorable coniditons for the grenadier, allowing some of the individuals to mature and spawn. /152

The scheme proposed above will probably be considerably expanded in future, especially with study of the grenadier of those regions which have not been considered in this work because of the lack of materials. We also cannot exclude the possibility of passive transport of some part of the fishes living in the NWA to the spawning grounds of the ridge. It appears however, that sufficient data has already been accumulated to make a judgement on some important problems, particularly, those involving the necessity of determining possible removals on the MAR, taking into account the fact that the grouping of this region also ensures the recruitment of the population of the NWA, and consequently, the possibilities of a grenadier fishery in the waters of Canada.

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